Assessing spillover from Marine Protected Areas and its drivers: a meta-analytical approach

Running title: Spillover from marine protected areas

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Keywords: Coastal, coral reefs, temperate reef, fully protected areas, no-take zone, marine reserve, fish, small-scale fisheries

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Abstract

The ocean offers vital ecosystem services to mankind. However, human activities, especially overfishing, may seriously impact populations ~~of exploited species~~ and ecosystems. Fully protected areas (FPAs) are an effective tool for biodiversity conservation and can sustain local fisheries via spillover, i.e. the export of juvenile and adult individuals from FPAs outwards. Yet, whether or not spillover, ~~or at which spatial scales,~~ is a general phenomenon following the establishment and effective management of an FPA is still controversial. Here, we developed a meta-analysis of a unique global database covering 23 FPAs in 12 countries, including both published literature and specifically collected field data, to assess the capacity of FPAs to export biomass and whether this response was mediated by specific FPA features (e.g. size, age) or species characteristics (e.g. mobility, economic value). Results, on average, show that fish biomass and abundance outside FPAs are clearly higher: i) in locations close to FPA borders (<200m) than in locations further away (>200m); ii) for species with a high commercial value; iii) in the presence of a partially protected area (PPA) surrounding the FPA. Age and size, as well as the FPA location (coastline vs island), played a slightly detectable role. Species mobility and habitat continuity across the FPA borders marginally affected spillover. ~~The meta-analytical approach we presented~~Our work grounds on the broadest dataset compiled to date on marine species ecological spillover beyond FPAs' borders and highlights ~~suggests some aspects~~elements that ~~to~~ could ~~enhnace~~enhance local fishery management.

TABLE OF CONTENTS

1. INTRODUCTION

Human activities are leading to dramatic modifications of the ocean (McCauley et al., 2015) and ~~. Overfishing~~ overfishing is among the most damaging stressors on marine biodiversity (IPBES, 2019). However, fisheries, especially small scale fisheries, are valuable economic activities, often vital for food security and poverty alleviation, and sources of livelihood with strong socio-cultural implications in coastal areas worldwide (Cisneros-Montemayor, Pauly, & Weatherdon, 2016). There is, therefore, an urgent need to identify management strategies able to reconcile conservation and fisheries goals by both protecting marine biodiversity and enhancing fishing yields/revenues (Gaines, Lester, Grorud-Colvert, Costello, & Pollnac, 2010; Jupiter et al., 2017).

Marine protected areas (MPAs) are widely recognized as an important tool for biodiversity conservation (Claudet et al., 2008; Edgar et al., 2014; Giakoumi et al., 2017) and fisheries management (Abesamis, Russ, & Alcala, 2006; Goñi et al., 2008; Russ & Alcala, 2011). MPAs can combine conservation and sustainable use goals by containing both fully protected areas (FPAs), where all extractive activities are forbidden, and partially protected areas (PPAs), where small scale ~~fishery~~ fisheries (SSF) are allowed, usually under more stringent regulations than ~~but they should be more strictly regulated than~~ outside ~~their~~ MPAs’ borders (Di Franco et al., 2016; Horta e Costa et al., 2016; Zupan, Fragkopoulou, et al., 2018). However, how ubiquitous are fishery benefits delivered by MPAs, for instance for highly mobile fish species and/or where there is strong fisheries management to prevent overfishing, is largely debated (Hilborn, 2016; Kerwath, Winker, Götz, & Attwood, 2013; Sale et al., 2005).

There is a body of evidence suggesting that FPAs can play an important role for fisheries management, especially for SSF (Di Franco et al., 2016; Januchowski-Hartley, Graham, Cinner, & Russ, 2013; Russ & Alcala, 2011). Two ecological processes can drive fishery benefits of FPAs: population replenishment through larval subsidies (Manel et al., 2019; Marshall, Gaines, Warner, Barneche, & Bode, 2019) and the spillover of fish biomass from protected areas to surrounding fishing grounds (Rowley 1994). While both processes require populations to firstly recover within the boundaries of the FPAs, generally the former is key to the long-term persistence of exploited populations also at relatively large distance from the MPA (i.e. hundreds of kms, Manel *et al.* 2019), while the latter produces faster benefits to fisheries ~~but~~ mainly across shorter distances (Halpern, Lester, & Kellner, 2010). The spatio-temporal scale of these two processes is species-specific (Green et al., 2015; McCauley et al., 2015).

The occurrence and magnitude of spillover is variable and context-dependent (Di Lorenzo, Claudet, & Guidetti, 2016). The maximum distance from FPA borders at which spillover effects are still detectable is a crucial issue to better understand the spatial extent of FPA benefits to local fisheries. Most studies found that spillover occur on average at distances of about 200 m from FPAs' borders, and all agree that it does not exceed 1 km (Abesamis et al., 2006; Abesamis & Russ, 2005; Guidetti, 2007; Halpern et al., 2010; Marques, Hill, Shimadzu, Soares, & Dornelas, 2015; Russ & Alcala, 2011). According to Di Lorenzo et al. (2016), two types of spillover should be considered on the basis of their assessment: "ecological spillover" encompassing all forms of net emigration of juveniles, subadults and/or adults from the MPA outwards; "fishery spillover", i.e. the fraction of ecological spillover that can directly benefit fishery yields and revenues through the marine species biomass that can be fished (Di Lorenzo et al 2016).

Spillover is not only important for local SSFs, but also for tourism-based blue economy. More abundant and larger fish exported from FPAs (where scuba-diving is often forbidden) attract more divers, thus supporting the local economy (Micheli & Niccolini, 2013; Roncin et al., 2008).

The overall relative contribution of potential drivers of spillover is poorly known. Two main categories of drivers may ~~facilitate~~ affect spillover: (i) MPA features: age, design (e.g. size, shape, location), presence of PPAs, the level of enforcement, habitat continuity/discontinuity across FPA borders (Goñi et al., 2008; Harmelin-Vivien et al., 2008; Kaunda-Arara & Rose, 2004; Kay et al., 2012); (ii) species characteristics: the species-specific ability to move across the FPA borders, related, e.g., to the intraspecific behaviour of individuals, habitat preferences and species mobility, fishing pressure (Kaunda-Arara & Rose, 2004). Some studies reported that spillover may require several years (>10 years) to take place after a FPA is established ~~(>10 years,~~ (Abesamis et al., 2006; Harmelin-Vivien et al., 2008; Russ & Alcala 1996; Russ, Alcala, & Maypa, 2003), while others detected spillover after only a few years from FPA creation (< 5 years; (Francini-Filho & Moura, 2008; Guidetti, 2007). Spillover has been observed from FPAs surrounded or not by a PPA (Abesamis et al., 2006; Francini-Filho & Moura, 2008; Harmelin-Vivien et al., 2008; Zeller, Stoute, & Russ, 2003) and detected both from small (< $1 km^2$; (Abesamis et al., 2006; Harmelin-Vvivien et al., 2008; Russ & Alcala 1996; Russ et al., 2003) and large FPAs (Ashworth & Ormond, 2005; Fisher & Frank, 2002; Stobart et al., 2009).

Habitat continuity inside and outside the FPA is thought to facilitate spillover (Abesamis & Russ, 2005; Kaunda-Arara & Rose, 2004), but several studies detected spillover also where the habitat was discontinuous across FPA borders (Goñi, Quetglas, & Reñones, 2006; Guidetti, 2007; Harmelin-Vivien et al., 2008; Kay et al., 2012). Spillover is expected to occur mostly for relatively mobile species (Buxton, Hartmann, Kearney, & Gardner, 2014; Halpern et al., 2010), but some studies showed that ~~also~~ sedentary, (Chapman & Kramer, 1999; Eggleston, & Parsons, 2008; Forcada et al., 2009; Goñi et al., 2008; Goñi et al., 2006; Zeller et al., 2003), vagile, (Abesamis et al., 2006; Forcada, Bayle-Sempere, Valle, & Sánchez-Jerez, 2008; Guidetti, 2007), and highly vagile species, (Chapman & Kramer, 1999; Kaunda-Arara & Rose, 2004; Stobart et al., 2009) may spillover beyond FPA borders.

Here, we performed a meta-analysis to 1) investigate the extent of spillover occurrence from FPAs globally and 2) assess which FPA features and species characteristics mainly drive spillover. To do so, we compiled the most complete global database on spillover, covering 23 FPAs in 12 countries, combining information from reviewed literature and data gathered through specific underwater visual census samplings on the field.

2. METHODS

2.1. Data collection

We assembled our dataset using two different approaches: extracting data from literature and performing *ad hoc* field activities to collect new data.

Articles on spillover from published peer-reviewed literature were collected through Web of Science back to 1994, when the term spillover was used for the first time (Rowley 1994). The following search string was used: (“spillover” OR "spill-over" OR "spill over") AND ("marine protected area*" OR "marine reserve*" OR "no-take zone*" OR "fisher* closure*” OR “fully protected area*”). It was decided to focus strictly on FPAs as this protection level is the more likely to produce spillover effects (Di Lorenzo et al., 2016 and references therein). Sixty-three studies of empirical assessments of spillover were found. They were either based on underwater visual census (UVC), catch or tagging abundance and/or biomass data. Spillover has been modelled in various ways in the literature, such as using linear gradients of abundance/biomass decline from FPA borders (e.g. (Goñi et al., 2006; Harmelin-Vivien et al., 2008) or tracking individual movements across FPA borders (Afonso, Morato, & Santos, 2008; Barrett, Buxton, & Gardner, 2009; Follesa et al., 2011; Kay et al., 2012; Kerwath et al., 2013). In order to keep the maximum number of studies, we built a model of spillover that would be as inclusive as possible in terms of different measurements and ways to report the data. Data from papers were extracted either from tables or from graphs using ImageJ (http://imagej.nih.gov/ij). Contextual information about the FPAs was recorded from the articles and/or by contacting their authors: FPA age and size, whether the FPA was situated ~~around a whole~~on an island or along a coastline, presence of PPA surrounding the FPA, and habitat continuity/discontinuity along FPA borders (Table 1). Information on species mobility (sedentary or vagile) and economic value (commercial, low commercial or not commercial) was also collected from the papers or FishBase (http://www.fishbase.org). It is worth noting that juveniles of target species were also included in the low commercial category as during that life stage ~~of their life~~ they are not ~~a~~ fishery targets~~ for fishers~~.

To ~~enrich~~enhance the dataset, we conducted additional fieldwork in 13 FPAs in 6 countries. Data were gathered using underwater visual census (UVC). SCUBA diving was carried out on rocky substrates between 5 and 15 m deep, using 25x5 m strip transects parallel to the coast. Along each transect, the divers swam one way at constant speed, identifying all fishes encountered to the lowest taxonomic level possible and recording their number and size. Fish sizes were estimated visually in 2 cm increments of total length (TL) for most of the species, and within 5 cm size classes for large-sized species (i.e. with maximum size >50 cm). Fish biomass was estimated from size data by means of length-weight relationships from the available literature and existing databases. UVC replicates (from 6 to 12 transects) were carried out close and far from FPAs borders, according to the rationale we used to detect spillover (see section 2.2~~below~~).

A total of 334 assessments from 23 MPAs (all having a reasonable level of enforcement) and 31 taxonomic groups (including species, genus or family) worldwide were finally used in the meta-analysis (Fig. 1; Table 1; Supplementary material Table S1).

2.2. **Data analysis**

Spillover was investigated in terms of effect size, i.e. by modelling the log-relative difference in mean fish abundance and biomass between ~~close (<200 m) and far (>200 m)~~ locations close (<200 m) and far (>200 m) from the FPA borders. We set the threshold at 200 m because spillover is generally observed up to such a distance from FPA borders (Abesamis et al., 2006; Guidetti, 2007; Harmelin-Vivien et al., 2008; Russ et al., 2003; Russ & Alcala, 2011). This approach is conservative in the sense that it favours false negative (absence of detection of spillover if it occurs over larger spatial extents) over false positive (detection of spillover when it does not occur, or over spatial extents with no significance for fisheries management).

We used a weighted mixed-effects meta-analysis (Gurevitch & Hedges, 1999) to quantify the magnitude of spillover and asses its drivers. Two different meta-analyses were done on abundance and biomass. For each study *i*, the spillover effect size R_i of the studied species across the studied FPA was modelled as the natural logarithm response ratio (Gurevitch & Hedges, 1999; Osenberg, Sarnelle, & Cooper, 1997) of the mean abundance or biomass measured within 200 meters ($\bar{X}_{close,i}$) and over 200 meters ($\bar{X}_{far,i}$) from the FPA boundary:

$$R_i = \ln\left(\frac{\bar{X}_{close,i}}{\bar{X}_{far,i}}\right)$$

The within-study variance v_i associated to the effect sizes was calculated as follows:

$$v_i = \frac{sd^2_{close,i}}{n_{close,i} * \bar{X}_{close,i}} + \frac{sd^2_{far,i}}{n_{far,i} * \bar{X}_{far,i}}$$

where $sd^2_{close,i}$ and $sd^2_{far,i}$ are the standard deviations of $\bar{X}_{close,i}$ and $\bar{X}_{far,i}$, respectively, and where $n_{close,i}$ and $n_{far,i}$ are the associated sample sizes.

All effect sizes were weighted, accounting for both the within- and among-study variance components (Hedges & Vevea 1998). Models were fitted and heterogeneity tests were run to assess how MPA-level (FPA age and size, island or coastline FPA, presence of a PPA, habitat continuity/discontinuity along FPA borders) and species-level (mobility and economic) drivers could mediate spillover from FPAs (Table 1). Models fitting and heterogeneity tests were carried out using the metaphor package (Viechtbauer, 2015) in R (R Core Team 2016).

3. RESULTS

The literature and fieldwork data considered here addressed our study on the assessment of “ecological spillover”. In fact, after screening using the study inclusion criteria, only one study concerning fishery yield was found to be relevant and provided the required data for performing the meta-analysis.

Overall, we found 33% higher fish abundance and 54% higher biomass close to the FPA borders (<200m) compared to further away ($\bar{\bar{R}}$ = 0.29 ± 0.15 95% CI and $\bar{\bar{R}}$ = 0.43 ± 0.21 95% CI, respectively), indicating the general occurrence of spillover. However, effect sizes were heterogeneous across assessments (Q_T = 7314, df = 167, $p < 0.001$; Q_T = 7777, df = 164, $p < 0.001$; respectively) (Supplementary material Table S2).

The presence of a PPA around FPAs played an important role. Spillover was observed more often from those FPAs surrounded by or next to a PPA (Figure 1). Particularly, abundance and biomass were respectively 37% and 84% higher closer to rather than further away from the FPA boundaries (Supplementary Materials Table S3).

For abundance data, spillover was mostly observed in FPAs established along coastlines rather than in FPAs surrounding a whole island (Figure 1). This difference was not observed when considering biomass data (Figure 1; Supplementary material: Table S2).

The occurrence and magnitude of spillover was only slightly affected by the age or the size of the FPA. Although statistically significant, the effect of age was marginal both for abundance ($\bar{R}$= 0.008 ± 0.007 95% CI) and biomass

($\bar{R}$= 0.014 ± 0.010 95% CI). The effect of the size of the FPA played a limited but appreciable role only in the case of abundance ($\bar{R}$= 0.04 ± 0.03 95% CI for abundance; $\bar{R}$= 0.02 ± 0.03 95% CI for biomass).

Habitat continuity/discontinuity~~homogeneity/heterogeneity~~ across FPA borders did not seem to affect the occurrence of spillover, both for abundance (Q_E=6767.35; df=165; *p*=0.0001) and biomass (Q_E=7299.05; df=163; *p*=0.0001) (Figure 1).

Spillover density and biomass was detected either for sedentary or vagile species (Figure 1; Supplementary Material: Table S1). Only the high commercial value species showed a spillover effect from FPA in terms of both abundance and biomass (Figure 1; Supplementary Material: Table S1).

4. DISCUSSION

Our results showed that spillover of marine species, both in terms of abundance and biomass, can be expected as a general response of FPAs. Based on the data that we have been able to gather, ~~The~~ the present study focused on ecological spillover (*sensu* Di Lorenzo et al. 2016). We found only one study that ~~studied~~ assessed fisheries spillover (using yield as response variable), which precluded us to account for this component of spillover in our meta-analysis. More efforts should be directed towards assessing spillover through fish catches along gradients across MPA borders.

Our synthesis suggested that the several drivers, here examined, have played a different role in affecting spillover: highly clear, slightly and marginal. Particularly, this study points out that the ecological spillover is detectable (i.e. ~~mainly~~ higher densities/biomass in locations close to FPA borders (<200m) than in locations further away (>200m)), when a PPA surrounds the FPA and when the species of interest has a high commercial value; the age or size of the FPA as well as the FPA location (coastline vs island) slightly affected the magnitude of spillover; whether species are more or less mobile and habitat continuity across the FPA borders played a marginal role to affect spillover.

To the best of our knowledge this is the first study ~~included~~ considering the presence of PPA as potential driver of spillover ~~to perform a meta-analysis~~, as well as benthic habitat continuity. Our findings suggest that the presence of a PPA might help the net export of biomass through spillover (and consequently the detection of fish abundance and/or biomass in the water) from the FPA. However, it is crucial to highlight that these patterns can be affected/altered by the magnitude of fishing effort around FPAs (in PPAs or in unprotected areas, depending on MPA zonation scheme). Fishing the line, i.e. ~~fishers~~fishers' tendency to fish close to the boundaries of FPAs (Kellner, Tetreault, Gaines, & Nisbet, 2007), is a recognized activity occurring around FPAs. In the absence of a PPA, fishery activities around FPAs' borders are not subject to strict spatially-explicit regulations beside the ones imposed by national and international laws, generally resulting in a higher concentration of the fishing effort close to the FPA borders (Abesamis & Russ, 2005; Chapman & Kramer, 1999; Davidson, Villouta, Cole, & Barrier, 2002; Follesa et al., 2011; Russ & Alcala, 2011; Stamoulis & Friedlander, 2013). ~~We know that t~~The detection of ecological spillover could be negatively impacted by fishing pressure in the fished areas, but high fishing effort can also concentrate within PPAs leading ~~at~~ to negative consequences of fishing the line in terms of fisheries spillover (Figure 2) (Kleiven et al., 2019; Zupan, Fragkopoulou, et al., 2018).

Our findings can shed light on the results observed in a recent meta-analysis assessing the effectiveness of different levels of protection (Zupan, Bulleri, et al., 2018). While the authors observed that fully and highly protected MPAs ~~tend to always~~ harbour ~~more~~ higher fish abundance and biomass globally, they found that moderately protected areas are effective only when adjacent to a fully protected area. In the absence of spillover from the FPA, such moderately protected areas allow too much fishing activities to be effective. Spillover can thus be an important component driving the effectiveness of multi-zoned MPAs, allowing combinations of protection levels favouring both conservation and fishing access in partially protected area concentrating fishing (Zupan, Bulleri, et al., 2018).

We observed a slightly influence of time since protection (i.e. MPA age) on ecological spillover, ~~according to~~in agreement with what has been observed for the response to protection within the FPA boundaries (Claudet et al., 2008;

Edgar et al., 2014; Molloy, McLean, & Côté, 2009). This can be due to the fact that our synthesis included FPAs with a large variation in age (min=6 years, median=19 years, max=32 years).

According to Halpern et al (2010), highly valued species are often were the ones mostly targeted by extractive activities. For this reason, Tthese are also the species responding most favourably and most rapidly to MPA establishment (Claudet, Pelletier, Jouvenel, Bachet, & Galzin, 2006; Babcock et al., 2010; Kerwath et al., 2013). An important difference between our synthesis and that by Halpern et al. (2010) is that whereas their study focussed on highly value fish species only, our analysis, for the first time, integrated data of three commercial value categories of species (i.e. no value, low and high).

Differently to Halpern et al 2010, a slightly effect of FPA size on spillover was also found; it suggests that the set of MPAs included in our study cover a range of sizes representing a trade-off between the inclusion of the home ranges of most species and the optimal size for spillover to neighbouring areas (Di Franco et al., 2018; Weeks, Green, Joseph, Peterson, & Terk, 2017). In fact, the size of a FPA should include the full home ranges of the protected species to obtain high conservation benefits (Di Franco et al., 2018; Weeks et al., 2017).

While several experimental studies have shown that homogeneous habitat continuity betweens inside and outside FPAs may play a role in facilitating spillover (Forcada et al., 2008; Goñi et al., 2008; Halpern et al., 2010; Kaunda-Arara & Rose, 2004), our meta-analysis showed that spillover could occur where the habitat across FPA borders is either homogeneous or heterogeneous. Such studies refer to the landscape connectivity theory ("the degree to which the landscape facilitates or impedes movement among resource patches"; Taylor *et al.* 1993), suggesting that similar habitat types across FPAs and fished areas may enhance the borders permeability (Bartholomew et al., 2008). However, our results suggest that the likelihood that fish cross a different habitat rather than the preferred one also depends on how fish can perceive and respond behaviourally to integrate the patched habitat to minimize overall costs (Bélisle, 2005; Wiens, 2008). Therefore, although different habitats outside FPAs could be a barrier to fish movements (due e.g. to the increased risk of predation), individuals may be able to move beyond FPA borders most likely when a threshold level of population density/biomass (i.e. competition for local resources such as preys and refuges) is exceeded.

In agreement with previous findings (Halpern et al., 2010), we observed that species, regardless of their mobility, are able to perform spillover. Contrary to Halpern et al. (2010) we decided to use only sedentary and vagile species in our analysis and removed the highly vagile species. The fact that any species with different mobility levels can display spillover may support the use of FPAs for coastal, SSF management, as these fisheries are multi-specific and usually target both sedentary and mobile species (Claudet, Guidetti, Mouillot, & Shears, 2011).

As in any qualitative review or quantitative synthesis or meta-analysis our study can harbour a publication bias. As studies evidencing spillover could be more likely published than those where no spillover is observed this would translate in some overestimation of spillover. However, our sample covers a large array of species, MPA types, and biogeographic regions and is well representative of spillover assessment in marine protection worldwide. Besides, the way we modelled spillover can in fact have led to underestimations. We are thus quite confident that MPAs, through spillover and larval subsidies (Marshall et al., 2019), can play a significant role in replenishing surrounding areas, therefore enhancing fisheries ~~management~~ and non-extractive activities that may benefit from increased fish density and biomass (e.g. scuba diving and tourism more in general).

In terms of socio-economic implications, therefore, the potential benefits induced by spillover could raise expectations in stakeholders (e.g. fishers, divers, tourists) that if shattered could induce a negative attitude and finally reduce support toward conservation initiatives and potentially foster non-compliant behaviours (e.g. poaching) (Bergseth, Russ, & Cinner, 2015). In our study we use a conservative approach to assess spillover occurrence (i.e. spillover might have been underestimated in some cases), and in addition we point out the circumstances under which spillover could occur, which is more appropriate from a management point of view as deception can be dramatic when a management tool is oversold (Chaigneau & Brown, 2016; Hogg, Gray, Noguera-Méndez, Semitiel-García, & Young, 2019). This can allow to deliver a clear message to stakeholders and avoid overselling the occurrence of spillover, preventing unrealistic expectations, and contributing to foster support to conservation initiatives (Bennett et al. 2019).

4.1. **Implication for management**

Our findings highlight under which conditions ~~beneficial~~ spillover may be expected, allowing MPA managers and policy-makers to develop sound management strategies to eventually maximise the exploitation of fishable biomass exported by FPAs. In fact, contrary to FPAs for which well-established regulations of human activities have been identified to reach conservation goals (essentially no extractive activities allowed), proven conditions for PPAs effectiveness are still scarce (in terms of which activities to allow and to which limits) (Zupan et al., 2018). Globally PPAs include a variety of management measures that range from almost unprotected areas (with no regulations implemented) to virtually FPA (Zupan et al. 2018). From this perspective, an effort should be made to assess under which conditions PPAs can benefit local communities within a multiple-use MPA. As PPAs currently lack a consistent and well-designed set of regulations worldwide (Horta e Costa et al., 2016), MPAs, mainly aimed to maximize fishery benefits, should assess the fisheries yield within PPAs and fished areas integrated with integrated with fishing ~~effort data~~effort data in order to optimise spillover (Figure 2).

ACKNOWLEDGEMENTS

We wish to thank N. Barrett, C. Bené, J. Bohnsack, E. Brunio, R. Cole, R. Davidson, D. Eggleston, R. Francini-Filho, D. Freeman, E. Hardman, F.A. Januchowski-Hartley, M. Kay, S. Kerwath,. D.L. Kramer, D. Malone, R. Ormond, M. Readdie, C. Roberts, A. Tewfik, K. Turgeon, M. Young, C. Wilcox and D. Zeller for sharing information about habitat types across MPAs borders. The authors would like to thank Prof. Paul Hart, and the two anonymous referees for their constructive comments and their kind help in improving the manuscript. We are grateful to Dr. Katie Hogg for her suggestions and editing of the English of the MS. MDL was supported by a "Luigi and Francesca Brusarosco" grant. FishMPAblue2 project (Interreg Mediterranean programme), Italian Marine Strategy monitoring, Foundation de France (INTHENSE), the ERA-Net

BiodivERsA (BUFFER) and the Agence Nationale de la Recherche (ANR-14-CE03-0001-01) for the Prince Albert II of Monaco Foundation (FPAII, Monaco) and the Total Corporate Foundation (France) financial support. Moreover, we are very grateful to all of MPAs directors and staff for their determining logistic and field support.

CONFLICT OF INTEREST: The authors declare that they have no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table 1. Empirical studies and data that met the section criteria of our meta-analysis. For further details, see the supplementary material.

N/A: Data Not Available

Fully protected area name (Country)	Years since enforcement	Reserve Size (km^2)	Presence of a partially protected area (PPA)	Number of species	Source
Apo (Philpines)	16	0.11	No	1	Russ and Alcala 1996; Russ *et al.* 2003, 2004; Abesamis and Russ 2005; Abesamis et al 2006; Russ and Alcala 2011
Asinara (Italy)	9	2.45	Yes	17	data collection
Balicasag (Philppines)	16	0.08	No	1	Abesamis et al 2006
Barbados (Caribbean)	15	2.3	No	Assemblage	Chapman and Kramer 1999
Bonifacio (France)	19	0.74	Yes	13	data collection
Cabo de Palos (Spain)	23	2.68	Yes	18	data collection
Cabrera (Spain)	22	0.85	Yes	Assemblage	Harmelin ~~vivien~~ Vivien et al 2008; Bellier et al 2013
Cap Roux (France)	15	0.44	No	12	data collection
Capo Carbonara (Italy)	6	0.6	Yes	16	data collection
Channel Islands (California)	7	N/A	No	1	Kay et al 2012a
Columbretes (Spain)	12	44	No	1	Goni et al 2006
Cote Bleue (France)	32	0.85	No	12	data collection
Egadi (Italy)	27	6.63	Yes	13	data collection
Mombasa (Kenya)	6	10	No	Assemblage	McClanahan and Mangi 2000
Portofino (Italy)	19	0.18	Yes	15	data collection
Pupukea-Waimea (Hawaii)	17	0.71	No	Assemblage	Stamoulis and Friedlander 2013
Strunjan (Slovenia)	10	0.46	Yes	7	data collection
Su Pallosu (Italy)	11	4	No	1	Follesa et al 2011
Tabarca (Spain)	20	14	Yes	1	Forcada 2008
Telascica (Croatia)	30	0.12	Yes	13	data collection
Tonga (Tonga)	7	18.35	No	1	Davidson *et al.* 2002
Torre Guaceto (Italy)	18	1.38	Yes	12	Guidetti *et al.* 2007; data collection
Zakyntos (Greece)	19	8	Yes	10	data collection

Figure Captions

Figure 1: MPA-level and species-level drivers of spillover. The spillover indicator is the log-transformed ratio of fish biomass or abundance between close and far from fully protected area boundaries (average weighted effect size +/- 95% CI). Green dots indicate effect sizes that do not overlap zero and red dots those that overlap zero.
Heter.: Heterogeneous; Homog.: Homogeneous

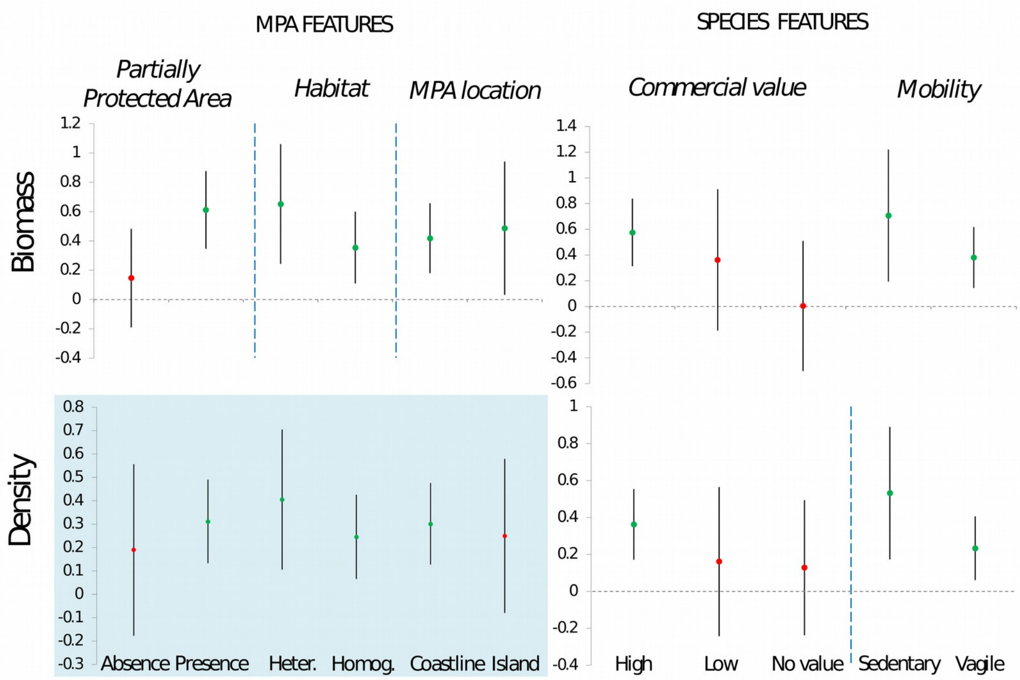

Figure 2: This generic conceptual framework illustrates the potential effects of presence and absence of partially protected area (PPA) surrounding fully protected area (FPA) on spillover. Three different scenarios are shown: A) high fishing pressure could reduce the ecological and fishery spillover assessment in fished area around FPA; B) high fishing pressure could reduce the ecological (standing stock biomass) and fishery (catches) spillover assessment within PPA surrounding the FPA and nullifies both spillover assessment in fished area; C) low fishing pressure could increase the ecological and fishery spillover assessment within PPA surrounding the FPA and enhances ecological and fishery spillover assessment in the fished area